Research article

Impacts of grazing exclusion on productivity partitioning along regional plant diversity and climatic gradients in Tibetan alpine grasslands

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ABSTRACT

The biodiversity-productivity relationship is critical for better predicting ecosystem responses to climate change and human disturbance. However, it remains unclear about the effects of climate change, land use shifts, plant diversity, and their interactions on productivity partitioning above- and below-ground components in alpine grasslands on the Tibetan Plateau. To answer this question, we conducted field surveys at 33 grazed vs. fenced paired sites that are distributed across the alpine meadow, steppe, and desert-steppe zones on the northern Tibetan Plateau in early August of 2010–2013. Generalized additive models (GAMs) showed that aboveground net primary productivity (ANPP) linearly increased with growing season precipitation (GSP) while belowground net primary productivity (BNPP) decreased with growing season temperature (GST). Compared to grazed sites, short-term fencing did not alter the patterns of ANPP along climatic gradients but tended to decrease BNPP at moderate precipitation levels of 200 mm < GSP < 450 mm. We also found that ANPP and BNPP linearly increased with species richness, ANPP decreased with Shannon diversity index, and BNPP did not correlate with the Shannon diversity index. Fencing did not alter the relationships between productivity components and plant diversity indices. Generalized additive mixed models furtherly confirmed that the interaction of localized plant diversity and climatic condition nonlinearly regulated productivity partitioning of alpine grasslands in this area. Finally, structural equation models (SEMs) revealed the direction and strength of causal links between biotic and abiotic variables within alpine grassland ecosystems. ANPP was controlled directly by GSP (0.53) and indirectly via species richness (0.41) and Shannon index (−0.12). In contrast, BNPP was influenced directly by GST (−0.43) and indirectly by GSP via species richness (0.05) and Shannon index (−0.02). Therefore, we recommend using a joint approach of GAMs and SEMs for better understanding mechanisms behind the relationship between biodiversity and ecosystem function under climate change and human disturbance.

1. Introduction

The biodiversity-productivity relationship is one of the fundamental questions in nature conservation under climate change (Chapin et al., 2000; Loreau, 2000; Loreau et al., 2001). The shape of such a relationship varies from being linear to unimodal (sometimes called hump-backed pattern), or even there is no significant correlation between biodiversity and productivity (Grace, 1999; Waide et al., 1999). Therefore, no agreement is reached on the mechanisms underlying the biodiversity-productivity relationship yet (Hooper et al., 2005; Isbell et al., 2015; Naeem and Wright, 2003).

The complexity of the mechanisms behind such a relationship is likely because biotic and abiotic regulators are always interacted to affect both biodiversity and productivity simultaneously (Tilman et al., 2012). As theory predicts, ecosystem functioning, i.e., productivity, is not necessarily to linearly respond to changes in species diversity, and nonlinear patterns are also possible for the biodiversity-productivity relationship and shaped by species coexistence (Baert et al., 2017; Tredennick et al., 2017). The nonlinear relationship between biodiversity and ecosystem functions are finally weaved into a complicated network of ecosystem responses to external disturbances, i.e., grazing and fertilizing in grasslands (Saatkamp et al., 2010; Tian et al., 2016).

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Main abbreviations

		turnover rate
AIC	Akaike Information Criterion	
AGB	above-ground biomass, g m^{-2}	GAM — generalized additive model
AGTs	alpine grassland types, here refer to meadows, steppes, and desert-steppes on the northern Tibetan Plateau	GAMM — generalized additive mixed model
ANPP	above-ground net primary productivity, equaling to peak AGB, g m^{-2}	GSP — growing season precipitation, sum precipitation during the plant growing season from May to September, mm
BGB	below-ground biomass, equaling to alive root biomass at the topsoil layer of 0–20 cm, g m^{-2}	GST — growing season temperature, the average temperature during the plant growing season from May to September, °C
BNPP	below-ground net primary productivity at the layer of 0–20 cm, g m^{-2}, estimated with ANPP, BGB, and root	LUTs — land use types, here refer to grazing and fencing. Fencing also means that the grassland is protected and non-grazed
		SEM — structural equation model
		SRMR — standardized root-mean-square residual

Therefore, merging the concepts of nonlinearity and complexity into ecosystem models is critical for better predicting the climatic and anthropogenic impacts on ecosystem service and functions.

Alpine grasslands on the Tibetan Plateau are sensitive and vulnerable to climate change and livestock grazing (Harris, 2010; Shang et al., 2014; Zhang et al., 2015). The biodiversity-productivity relationship has been reported as linear or unimodal patterns for alpine grasslands on this plateau (Ma et al., 2010; Shi et al., 2014; Wang et al., 2013). Due to the release of select grazing by livestock, species of sedges and grasses benefited from short-term fencing, with increased biomass and dominance (Wu et al., 2014a, 2014c). Thus, the relationship between biodiversity and productivity is predicted to be different between grazed and fenced communities due to the altered species assembly. However, scientists recently found that short-term fencing had no impacts on the diversity-productivity relationship for alpine grasslands on the northern Tibetan Plateau (Yan and Lu, 2015). The disagreement between theoretical predictions and practical observations is likely due to the poor predictivity of the bivariate model. For example, Grace et al. (2014) have suggested that a simple bivariate model can not explain the nonlinearity and causality of ecosystem dynamics.

In this study, we mainly aim to explore the biodiversity effects on productivity partitioning above- and below-ground components across alpine grasslands under grazing and fencing. Here, we hypothesize that (1) plant species diversity and productivity partitioning respond to regional climatic changes nonlinearly; (2) fencing (with grasslands being protected and non-grazed) relative to grazing, significantly alters the manners of plant species diversity and productivity components in response to climatic changes, as well as their relationships; and the (3) climatic variables regulate productivity components between above- and below-ground, directly and indirectly via different biodiversity effects.

2. Materials and methods

2.1. Study area

This study was performed on the northern Tibetan Plateau, which is a hotspot for biodiversity conservation under climate change (Li et al., 2018). In the past decades, this area became much warmer than the other parts of the Tibetan Plateau, with the warming rates as nearly three times the global average (Yao et al., 2012; Yu et al., 2016). Overgrazing and warming have caused about 15.3 million hectares of grassland degradation, which accounts for about one-quarter of available pastures in this area (Yu et al., 2016). From 2006 to 2012, about 3.3 million hectares fences were constructed for grazing exclusion in severely degraded grasslands (Yu et al., 2016).

In spring 2009, we established a 1200 km transect across the northern Tibetan Plateau for long-term research (Fig. 1). The primary aim was to study the potential mechanisms behind grassland degradation under grazing and restoration by fencing under climate change. Along with this transect, three zonal alpine grassland types (AGTs)

–meadow, steppe, and desert steppe–are involved from east to west. The total number of sites per each type are shown in Table 1, and the site distribution can also be found in the maps of Fig. 1. Dominant species varies from *Kobresia pygmaea* C.B. Clarke (average coverage of 70%) in meadows (canopy coverage of 65–95%), *Stipa purpurea* Griseb (average coverage of 35%) in steppes (canopy coverage of 30–60%), to *S. purpurea* and *S. glareosa* P. Smirn (average coverage of 25%) in desert-steppes (canopy coverage of 15–40%). Principal livestock also shifts from yaks in the cold, wet alpine meadow zone to sheep in the warm, semi-arid alpine steppe zone and then to goats in the hot, arid desert-steppe zone.

Along with this transect, site locations were suggested by the local authorities, and their suggestions were motivated by the extent of grassland degradation before fence constructions. In this study, the
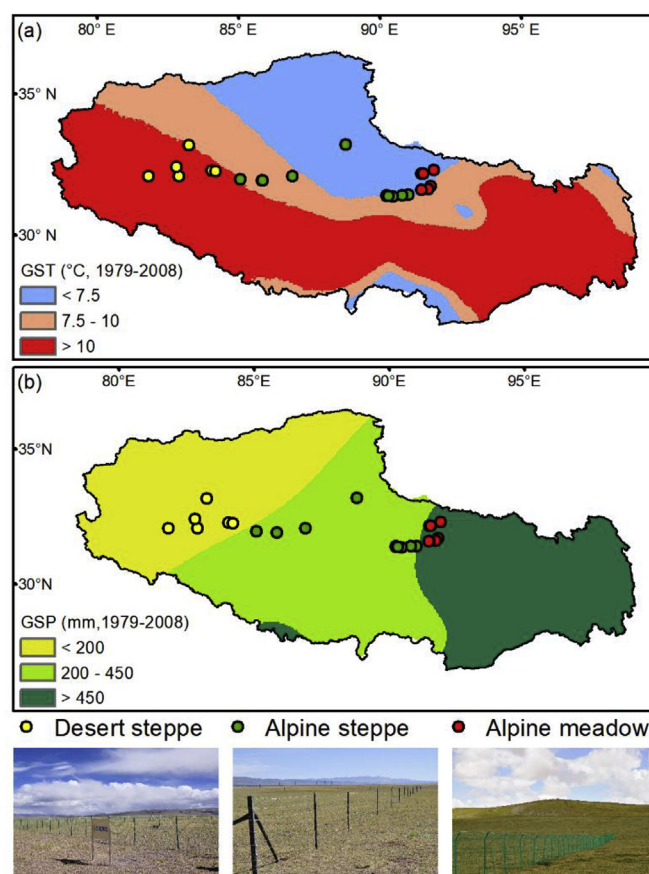

Fig. 1. Site locations in desert steppes, alpine steppes, and alpine meadows along climate gradients on the northern Tibetan Plateau. Panels (a) and (b) indicate growings season temperature (GST) and growing season precipitation (GSP) of 1979–2008, respectively.

Table 1
Location, climate and vegetation information across study sites on the Northern Tibetan Plateau.

AGTs	Sites	Longitude (°E)	Latitude (°N)	Altitude (m)	GSP (mm)	GST (°C)	ANPP (g m^{-2})	BNPP (g m^{-2})	Species richness (num m^{-2})	Shannon index (unitless)
AM	11	91.5–91.9	31.5–32.3	4531–4730	346.8–490.1	6.1–8.4	69.82 ± 5.93	151.61 ± 20.61	10.31 ± 0.63	1.78 ± 0.12
AS	16	85.1–91.0	31.4–33.2	4541–4995	200.1–455.0	5.2–11.1	31.45 ± 2.74	104.86 ± 13.37	6.14 ± 0.42	1.26 ± 0.09
DS	6	81.8–84.2	32.1–33.2	4440–4671	148.6–210.9	9.7–12.0	13.71 ± 1.82	75.26 ± 14.18	3.37 ± 0.33	1.00 ± 0.11

Alpine grassland types (AGTs) included alpine meadow (AM), alpine steppe (AS), desert steppe (DS). The ranges of site longitudes, latitudes, and altitudes, and growing season precipitation (GSP) and temperature (GST) were shown. Mean ± SE were calculated for above- and below-ground net primary productivity (ANPP and BNPP), species richness, and Shannon diversity index.

fenced plots were strictly limited to those had been excluded from livestock grazing all year round since autumn 2006 or spring 2007. The grazed plot at each site was chosen randomly within one or two kilometers away from the fenced one. Thus, we ensured that there was no large heterogenicity in soil and climate conditions between fenced and grazed plots. Meanwhile, the local authorities and pastoral families also promised that the open grasslands we chose for research would be not grazed until field samplings in each summer. Thus, we also avoided underestimating grassland productivity at grazed plots. Therefore, it makes sense to consider fencing and grazing as different land use types (LUTs).

2.2. Field survey and measurement

We performed in-*situ* observations at sites with grazing vs. fencing matched plots annually in each summer. Most annual herbaceous plants sprout in May and senesce in September on the northern Tibetan Plateau, and this period is usually used as the plant growing season (Shen et al., 2015; Wang et al., 2013). Plant coverage and biomass peak in late July or early August in the middle of plant growing season (Ma et al., 2010), and thus peak aboveground biomass (peak AGB) can be accepted as a proxy for aboveground net primary productivity (ANPP).

At each plot, five 0.25-m^2 subplots were located along a random sampling line at 20 m intervals within a flat area of 200 m × 200 m. Within each subplot, plant coverage was estimated and recorded for each species. Peak AGB was harvested with scissors at the soil surface and stored in separate envelopes by species. One soil block of 25 cm × 25 cm × 20 cm (length × width × depth) was sampled from the center of each subplot for estimating belowground biomass (BGB), the living root biomass. About 85% of living roots concentrate at the topsoil layer (0–20 cm) in alpine grasslands on the northern Tibetan Plateau (Li et al., 2011).

In the lab, root samples were thoroughly cleaned to remove soil particles and small stones under running water. After that, living roots were distinguished from dead ones by hand, according to their differences in color, elasticity, and attachment of fine roots. Finally, all of the above and below-ground plant samples were oven-dried at 65 °C for 48 h and weighted.

2.3. Data management and processing

To avoid the influence of outliers, we used the average values of above- and belowground biomass and plant diversity indices of the five subplots within each plot for statistical analysis. Belowground net primary productivity (BNPP) was estimated with the methodologies recommended by Gill et al. (2002) for grasslands globally (Eqns. (1) and (2)), where BGB and ANPP, respectively, were assumed to be the living root biomass and peak AGB. Regarding plant diversity indices, the number of all species occurring within the five subplot was used as species richness (*SR*). Species relative coverage (P_i) was used for calculating the Shannon diversity index (Eqn. (3)). In this study, we didn't include the evenness index because Pielou evenness of alpine grasslands in this area showed similar patterns to the Shannon diversity index along temperature and precipitation gradients in this area (Wu et al.,

2012). In a recent study, Yan and Lu (2015) also found that short-term fencing might have no influences on diversity indices, species richness, Shannon diversity index, Pielou Evenness and Simpson's dominance index.

$$BNPP = BGB \times turnover \qquad (1)$$

$$turnover = 0.0009 gm^{-2}(ANPP) + 0.25\ yr^{-1} \qquad (2)$$

$$H = -\sum_{i=1}^{SR} P_i \ln P_i \qquad (3)$$

Daily meteorological records were downloaded from China Meteorological Data Service Center (CMDC, http://data.cma.cn). Chen et al. (2014) have already generated monthly raster surfaces of temperature and precipitation with ANUSPLIN 4.3 at a spatial resolution of 1 km × 1 km (Hutchinson, 2004) and found that the interpolated climatic values agreed well with field observations across the northern Tibetan Plateau. Therefore, we used these climate raster data of Chen et al. (2014) to calculate mean temperature and sum precipitation during the plant growing seasons (noted as GST and GSP, respectively) and then extracted for each site according to their geographic coordinates in ArcGIS 10.2.

Soil total carbon and nitrogen were not included in the statistical analyses because of collinearity between explanatory factors (Dormann et al., 2013; Graham, 2003) that soil carbon and nitrogen contents were highly correlated with climatic factors (especially with GSP) (Wu et al., 2016). Besides, short-term fencing (less than five years) did not change soil chemical and physical characteristics in this study area (Lu et al., 2015a).

2.4. Statistical analysis

First, we used the thin plate regression splines with the *mgcv* package (Wood, 2012) to uncover the nonlinearity of productivity partitioning and plant species diversity indices in response to regional changes in climatic variables. The thin plate regression spline is recommended by Wood (2012) for it tends to give the best Mean Square Error performance.

Second, generalized additive mixed models (GAMMs) were used to examine if fencing relative to grazing has altered the responses of productivity partitioning and plant diversity indices to regional climate change. In this step, the estimated trend of the response variable across grazed plots was viewed as the reference for comparisons. The difference of the estimated trends between fenced and grazed plots was used to indicate how fencing affects productivity partitioning or plant diversity against climatic gradients. Similarly, we also examined the land use effects, fencing vs. grazing, on the relationships between productivity components and plant diversity indices.

Finally, the spatial complexity of localized interactions between climate and plant diversity on productivity partitioning were examined by using the function of tensor product smooths within the *mgcv* package (Wood, 2012). Besides, full-factorial SEMs with the *lavaan* package (Rosseel, 2012) were used to examine the causal links between climate variables, plant diversity indices, and productivity components.

A backward selection process according to the Akaike Information Criterion (AIC) was performed to pick out the optimal GAMs and SEMs. This method drops the least significant explanatory term or paths, refits the model, and continues until all terms or paths are significant at the 0.05 level (Zuur et al., 2009). The Chi-square (χ^2) test with $p > 0.05$ and the standardized root mean square residual (SRMR) ≤ 0.05 indicate SEM results to be acceptable (Fan et al., 2016). All statistical analyses were performed in the environment R 3.3.3 (R Core Team, 2017).

3. Results

3.1. Spatial patterns of productivity components along climatic and plant diversity gradients

ANPP across grazed and fenced grasslands increased with increasing GSP linearly (Fig. 2a). ANPP showed a unimodal pattern with increasing GST across the fenced plots, but first decreased and then followed a unimodal pattern with increasing GST across the grazed plots (Fig. 2b). BNPP showed a unimodal flatting pattern with GSP across the grazed communities. However, BNPP showed a rapid increase where GSP was more than 400 mm across the fenced ones (Fig. 2c). BNPP across the fenced plots decreased with increasing GST linearly but across the grazed ones showed a unimodal pattern with the peak value at GST of 7 °C (Fig. 2d). The spatial patterns of species richness and the Shannon diversity index against climatic variables were shown in the supplementary file (Appendix Fig. S1).

ANPP linearly increased with species richness (Fig. 3a) and the Shannon diversity index (Fig. 3b) across the grazed and fenced plots. BNPP also increased with species richness (Fig. 3c) linearly. BNPP across the grazed plots increased with the Shannon diversity index slightly; however, there was no relation between BNPP and the Shannon diversity index across the fenced plots (Fig. 3d).

3.2. Effects of land use types on the relationship between productivity partitioning and climate

The estimated trend in ANPP was found to increase with increasing GSP significantly ($P < 0.001$, Table 2; Fig. 4a) but decrease with increasing GST non-significantly ($P > 0.05$, Table 2; Fig. 4b). Compared to the grazed plots, fencing did not significantly alter the estimated trends of ANPP along regional climate gradients ($P > 0.05$, Table 2). There was no evident trend in the difference of ANPP between the fenced and grazed plots against GSP (Fig. 4c) and GST (Fig. 4d).

There was no evident trend in BNPP with increasing GSP ($P > 0.05$, Table 2; Fig. 4e). The estimated trend in BNPP was found to decrease with increasing GST significantly ($P < 0.05$, Table 2; Fig. 4f). Compared to the grazed plots, fencing had significant influences on the manners of BNPP in response to GSP and GST ($P < 0.05$, Table 2). The estimated trend in the difference of BNPP between fenced and grazed plots first decreased and then increased with increasing GSP, with an inflection point nearby GSP of 400 mm (Fig. 4g). The estimated trend in the difference of BNPP between fenced and grazed plots decreased with increasing GST linearly (Fig. 4h). Fencing relative to grazing was found not to impact plant diversity indices (Appendix Fig. S2 c & g) with increasing GSP but was found to increase plant diversity indices with increasing GST (Appendix Fig. S2 d & g, and Table S1).

3.3. Effects of land use types on the relationship between productivity partitioning and plant diversity

The estimate trend of ANPP was found to increase with species richness linearly and to decrease with the Shannon diversity index ($P < 0.001$, Table 2, Fig. 5a–b). The estimated trend in BNPP was found to increase with species richness linearly ($P < 0.05$, Table 2; Fig. 5e) but no change with the Shannon diversity index ($P > 0.05$,

Table 2; Fig. 5f). Compared to the grazed plots, fencing had no effects on the manners of ANPP and BNPP in response to changes in species richness and the Shannon diversity index (ANPP, Fig. 5c–d; BNPP, Fig. 5g–h).

3.4. Spatial patterns of effects of interactions between climate and plant diversity on productivity partitioning

Except for the interaction between species richness and GSP had no significant impact on BNPP, other interactions between climate and plant diversity indices were found to affect productivity partitioning significantly (Table 3). With increasing species richness, ANPP increased in the cold meadow zone where GST was lower than 7.5 °C, decreased in the warm steppe zone where GST was between 7.5 °C and 10 °C, and kept consistent in the hot desert steppe zone where GST was higher than 10.0 °C (Fig. 6a). With increasing Shannon diversity index, ANPP increased in the arid desert zone where GSP was less than 200 mm, kept steady in the semi-arid steppe zone where GSP was between 200 and 400 mm, and decreased in the wet meadow zone where GSP was more than 400 mm (Fig. 6b). With increasing Shannon diversity, ANPP decreased more rapidly at the cold meadows (with the narrower distance between estimated isoclines) than at the warm steppes and hot deserts (with the broader distance between estimated isoclines, Fig. 6c). However, with increasing species richness, ANPP increased at the same rate across GSP gradients (equal width between estimated isoclines, Fig. 6d).

In the alpine grasslands with higher GST than 8 °C, BNPP showed no relationship with species richness but decreased with increasing GST. In contrast, BNPP in the alpine grasslands with GST lower than 8 °C decreased with increasing species richness (Fig. 6e). The spatial pattern of interacting effects between the Shannon diversity index and GST on BNPP (Fig. 6g) was similar to that of the interacting effects between species richness and GST (Fig. 6e). In the alpine grasslands with 250 mm < GSP < 425 mm, BNPP increased with increasing Shannon diversity index (Fig. 6f). The interactions of species richness and GSP
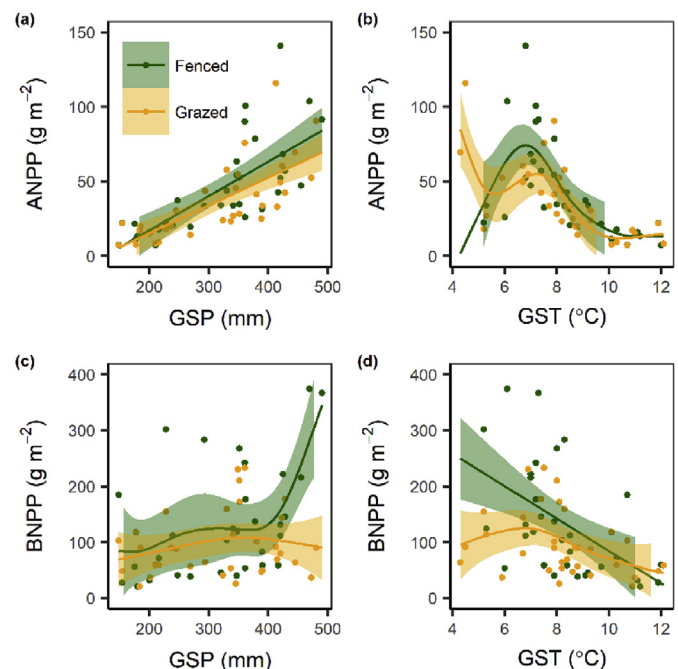

Fig. 2. Spatial patterns of productivity partitioning across fenced and grazed grasslands along climatic gradients in the northern Tibet Plateau. Estimated trends with 95% confidence intervals were generated by using thin plate regression splines in generalized additive models (GAMs) with *mgcv* and *ggplot* packages in R.
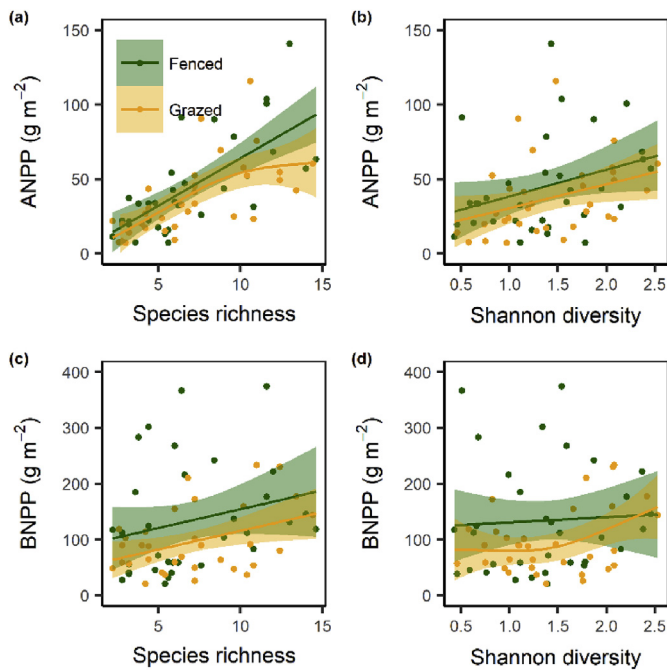
Fig. 3. Spatial patterns of productivity partitioning across fenced and grazed grasslands along plant diversity gradients on the northern Tibetan Plateau. Estimated trends with 95% confidence intervals were generated by using thin plate regression splines in generalized additive models (GAMs) with *mgcv* and *ggplot* packages in R.

did not significantly impact BNPP (Table 3) but showed a similar spatial pattern in influencing BNPP (Fig. 6h) to the interactions between Shannon diversity index and GSP (Fig. 6f).

3.5. Directions and strengths of influences of climate variables and plant diversity on productivity partitioning

Structural equation models clarified the direct effects of climate variables and their indirect effects interacting with plant species richness and Shannon diversity index on community productivity partitioning (Fig. 7). Individually, GSP controlled ANPP significantly via a standardized direct pathway of 0.53 in strength (Fig. 7a). Meanwhile, GST influenced BNPP significantly via a standardized direct pathway of −0.43 in strength (Fig. 7b). The indirect effects of GSP on ANPP via species richness and Shannon diversity index were 0.406 and −0.119 in strength, respectively (Fig. 7a). Although GSP had no direct influence on BNPP, the indirect effects of GSP through species richness and Shannon diversity index were considerable with 0.055 and −0.022 in

strength, respectively (Fig. 7b). The models considering the above- and below-ground feedback were shown in the supplementary file (Appendix Fig. S3), where the indirect influence of GSP via ANPP on BNPP (0.10) was twice the indirect influence of GST via BNPP on ANPP (−0.05) in strength.

4. Discussion

Grazing is a wide-spread disturbance on grassland ecosystems all over the world. Grazing can affect the performance of individual plants, community composition, and vegetation dynamics (Medina-Roldan et al., 2012; Semmartin et al., 2008; Veen et al., 2012). However, no agreement is reached whether fencing with livestock grazing excluded can significantly alter the shape of the biodiversity-productivity relationship in grasslands. In this case, we did not quantify how much biomass or the value of diversity index was reduced or enhanced due to fencing, compared to alpine grasslands under grazing on the northern Tibetan Plateau. Instead, we examined whether fencing relative to grazing altered the manner of productivity partitioning between above- and below-ground along the regional gradients of climatic variables and plant diversity indices. Finally, we uncovered the nonlinearity and complexity of the mechanisms behind the diversity-productivity relationship by using a joint approach of generalized additive modeling and structural equation modeling.

4.1. Effects of fencing vs. grazing on the responses of productivity partitioning to climate change

First, we observed linearity and non-linearity in both ANPP and BNPP varying along the regional gradients of temperature and precipitation (Fig. 2), which are consistent with previous studies on the Tibetan Plateau (Ma et al., 2010; Wang et al., 2013). The positive correlation between ANPP and precipitation (Fig. 2a) was also consistent with most studies in drylands (Austin and Sala, 2002; Golodets et al., 2013; Guo et al., 2012; Peters et al., 2014), indicating that water availability is the crucial limiting factor for ANPP in arid and semi-arid grasslands. Besides, we found unimodal patterns between ANPP and temperature at both fenced and grazed sites (Fig. 2b), suggesting warming might only favor alpine steppes in the central areas on the northern Tibetan Plateau (Fig. 1).

Some scientist observed that AGB was larger in fenced sites than the adjacent grazed ones on the northern Tibetan Plateau (Wu et al., 2014c; Xiong et al., 2014). However, the usability of AGB to indicate fencing effects on ecosystem restoration, relative to grazed grasslands, is further complicated by the facts that overgrazing has negative influences on plant growth but moderate levels of grazing can promote plant fitness and growth (Eldridge et al., 2017; Lezama et al., 2014; Pakeman, 2004; Ruppert et al., 2012; Zhang et al., 2018). Therefore, the difference in

Table 2
Approximate significance of climatic variables in the generalized additive mixed models (GAMMs) for productivity partitioning and plant diversity indices.

smooth terms	edf.	ref.df	F	P	edf.	ref.df	F	P
	GAMM1 for ANPP				GAMM2 for BNPP			
s(GSP)	**0.973**	**9**	**3.856**	**< 0.001**	0.000	9	0.000	0.547
s(GST)	0.774	9	0.145	0.180	**1.553**	**9**	**0.560**	**0.034**
s(GSP)_{fenced-grazed}	0.035	9	0.004	0.308	**3.373**	**9**	**2.005**	**< 0.001**
s(GST)_{fenced-grazed}	0.000	9	0.000	0.394	**0.839**	**9**	**0.576**	**0.012**
	GAMM3 for ANPP				GAMM4 for BNPP			
s(Richness)	**0.990**	**9**	**9.215**	**< 0.001**	**8.250e-01**	**9**	**0.524**	**0.020**
s(Shannon)	**2.352**	**9**	**3.728**	**< 0.001**	5.181e-05	9	0.000	0.563
s(Richness)_{fenced-grazed}	0.255	9	0.038	0.248	3.532e-05	9	0.000	0.687
s(Shannon)_{fenced-grazed}	0.000	9	0.000	0.563	3.004e-04	9	0.000	0.483

Estimated degree of freedom (edf), the referenced degree of freedom (ref.df), variance ratio (F) and significance level (P) are shown. The main effects of explanatory variables are given as s(factor). The interacting effect of a given influential factor with land use types is given as the estimated difference of trends in a given response variable between fenced and grazed plots, notated as s(factor)_{fenced-grazed}, where the estimated trend across the grazed plots is considered as the reference. Items in bold are shown for smooth terms being significant at P < 0.05.
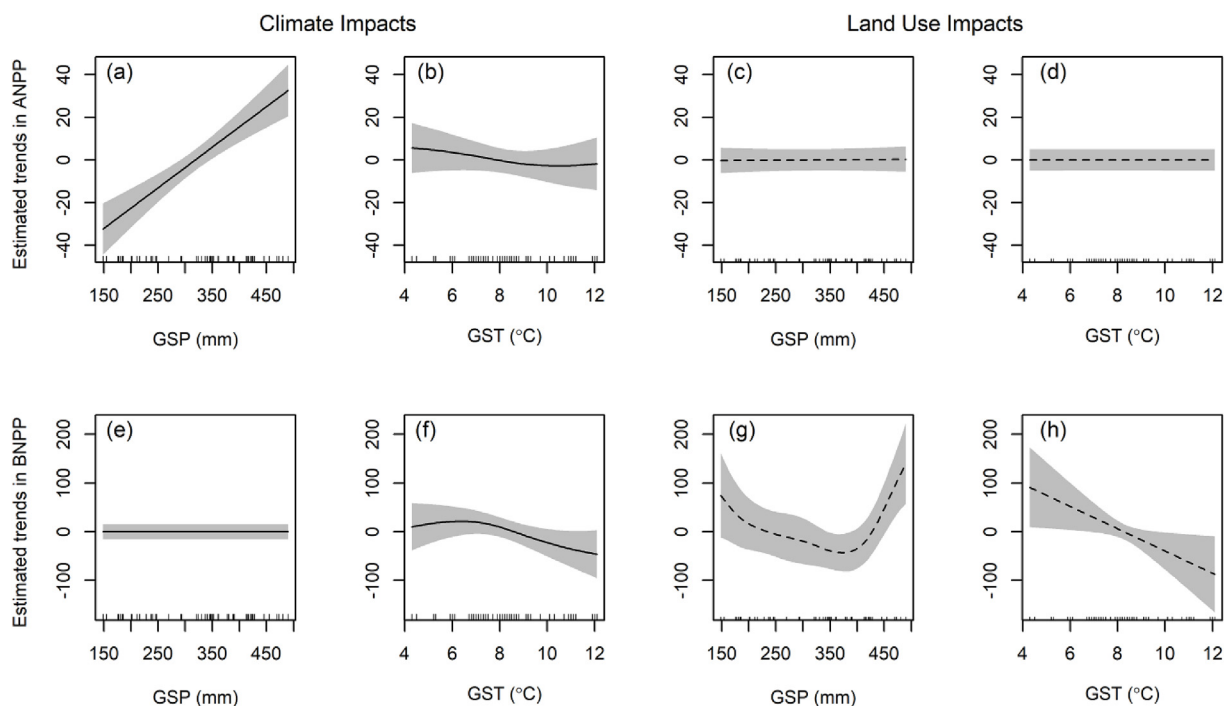
Fig. 4. Effects of climate and land use on productivity partitioning in alpine grasslands on the northern Tibetan Plateau. Estimated trends with 95% confidence intervals are shown in solid lines for main climate impacts (a–b & e–f) and dashed lines for interacting effects of climate × land use (c–d & g–h). See Table 2 for the model summary.

AGB between fenced and grazed plots, cannot robustly reveal whether fencing relative to grazing has altered grassland productivity because the proportion of consumption, compensation, and defoliation caused by large herbivores are challenging to be accurately estimated. In our case, the ANPP between fenced and grazed plots was comparable because livestock grazing was not allowed before field samplings even in

the grazed plots. Therefore, we can conclude that the short-term fencing (less than five years), relative to grazing, has no impacts on grassland restoration since the manners of ANPP responding to changes in precipitation and temperature (Fig. 4 c & d, dashed lines without any tendency) have not altered by fencing yet.

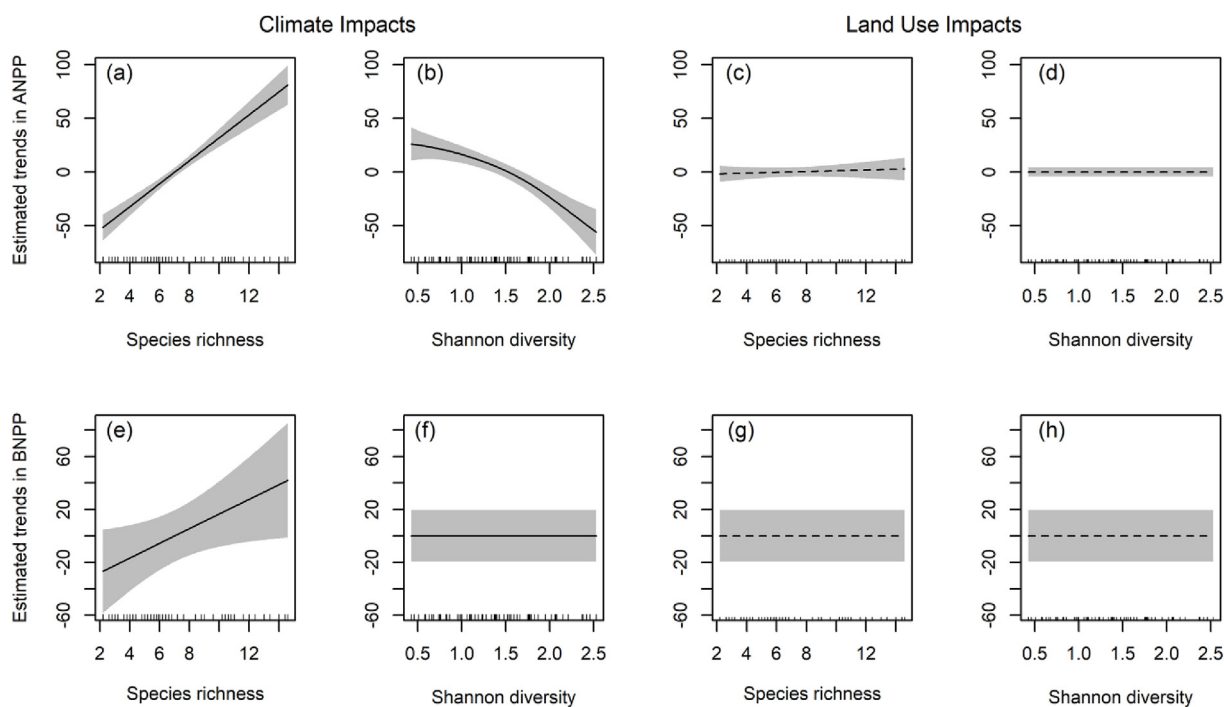To date, we know little about the fencing effects on BNPP for the

Fig. 5. Effects of plant diversity and land use types on productivity partitioning in alpine grasslands on the northern Tibetan Plateau. Estimated trends with the 95% confidence intervals are shown in solid lines for plant diversity impacts (a–b & e–f) and dashed lines for interacting effects of climate × land use (c–d & g–h). See Table 2 for the model summary.

Table 3
Approximate significance of the interacting effects between of climate variables and plant species diversity indices in generalized additive mixed models (GAMMs) on productivity partitioning.

smooth terms	edf.	ref.df	F	P	smooth terms	edf.	ref.df	F	P
GAMM5 for ANPP					GAMM6 for ANPP				
te (GST, Richness)	3.608	24	1.674	< 0.001	te (GST, Shannon)	3.491	23	0.569	0.004
te (GSP, Shannon)	2.495	24	1.079	< 0.001	te (GSP, Richness)	2.656	24	2.063	< 0.001
GAMM7 for BNPP					GAMM8 for BNPP				
te (GST, Richness)	3.559	23	0.724	< 0.001	te (GST, Shannon)	4.294	24	0.723	0.001
te (GSP, Shannon)	1.783	24	0.190	0.043	te (GSP, Richness)	0.810	23	0.054	0.177

Shown are the estimated degree of freedom (edf), the referenced degree of freedom (ref.df), variance ratio (*F*) and significance level (*P*). The interacting effects of any given influential factors, notated as te (factor 1, factor 2), are estimated by using the *mgcv* package in R, with the function for a full tensor product smooth.
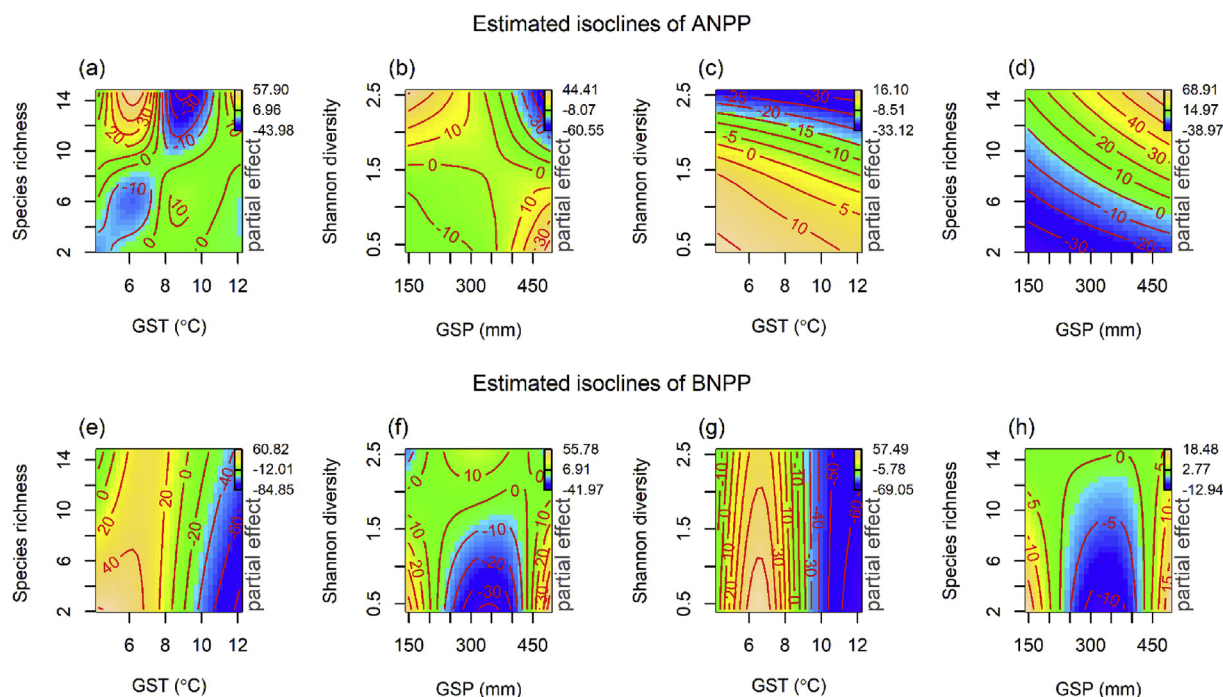

Fig. 6. Spatial patterns of interacting effects between climates and plant diversity on productivity partitioning in alpine grasslands on the northern Tibetan Plateau. Estimated isoclines are shown for the tensor product smooths generated by using the *mgcv* package in R. See Table 3 for the model summary.

Tibetan alpine grasslands because most studies only focused on BGB rather BNPP there. For example, Li et al. (2011) found that root biomass decreased exponentially with soil depths but was mainly concentrated at the topsoils of 0–20 cm layer. In this study, we found that fencing, relative to grazing, has significantly altered the manners of BNPP responding to changes in precipitation and temperature (Fig. 4 g & h). This is different from the study of Lu et al. (2015b) that five-year fencing might be too short to alter productivity partitioning. The mechanisms of grazing effects on root biomass or belowground biomass are complicated. It is generally agreed that the grazing effects on belowground processes are dependent on both the levels of grazing (Biondini et al., 1998) and the community composition (Ylanne et al., 2018). Our finding of the altered responses of BNPP to precipitation and temperature by fencing (Fig. 4 g & h) was also different from the study in Tanzania's Serengeti National Park where McNaughton et al. (1998) found that intense grazing did not inhibit root biomass or belowground productivity.

Soil carbon and nitrogen contents were found to be highly correlated with climatic factors (especially with precipitation) in this study area (Wu et al., 2016). In addition, such short-term fencing (less than five years) did not change soil chemical and physical characteristics in the same area (Lu et al., 2015a). Therefore, we cannot attribute the altered manners of BNPP by fencing in response to regional climatic changes to soil nutrient effects, although fencing might reduce the soil

nutrient effects on the trade-offs of biomass allocation between above- and below-ground (Sun et al., 2018). On the other hand, we do not think that the direct influences of plant diversity are essential for interpreting the altered manners of BNPP responding to climatic variables because fencing did not change the relationships of BNPP with plant diversity indices (Fig. 5 g & h). The reasonable explanations might be the interactions between climatic variables and plant diversity indices or the indirect influences of climatic variables through species assembly.

4.2. Effects of fencing vs. grazing on the relationships of productivity components with diversity indices

The linear relationships of productivity components with plant diversity indices (Fig. 3). Plant species diversity and community productivity are always correlated with the physical environment in natural ecosystems. A linear diversity-productivity relationship always occurs in ecosystems where both productivity and plant diversity respond to abiotic changes in similar ways (Loreau, 2000). However, a unimodal curve or nonlinear pattern always arose where diversity and productivity are in opposite or non-parallel directions in response to physical environmental changes (Ma et al., 2010; Wang et al., 2013). The relative independence of plant diversity and productivity from environmental changes influenced the shape of the relationship
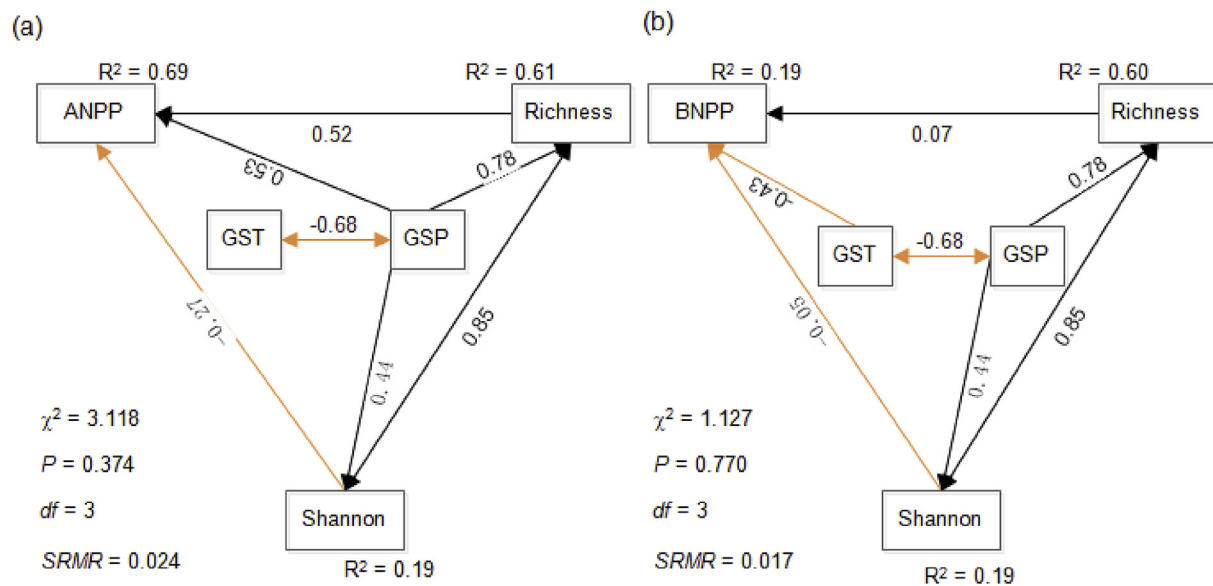
Fig. 7. Structural equation models revealed the direct and indirect influences of climate variables and plant diversity indices on productivity partitioning (a, ANPP; b, BNPP) of alpine grasslands on the northern Tibetan Plateau. Data are log10-transformed to mitigate the deviation from normality and linearity. Pathways in black and orange indicated positive and negative effects, respectively. Single-arrowed and double-arrowed pathways indicate the directional effect and correlation between variables, respectively. Values associated with pathways are the standardized path coefficients. The R^2 values are given for productivity, species richness, and the Shannon diversity index. The fitness statistics, chi-square (χ^2), the degree of freedom (df), P value and standardized root mean square residual (SRMR) are given for the fitness of the two models. The χ^2-test with $P > 0.05$ and the SRMR ≤ 0.05 indicates that the model is acceptable. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

between them. In our case, we can conclude that climatic variables are as critical in regulating species diversity as controlling community productivity on the northern Tibetan Plateau.

Regarding land use effects, we found that fencing did not alter the shapes of the relationships between plant diversity indices and productivity components (Fig. 5 c-d & g-h, and Table 2). This can be explained by two reasons. On the one hand, five-year fencing was too short to significantly change soil nutrients (Lu et al., 2015a) and plant community structure (Wu et al., 2014a; Yan and Lu, 2015). In our study, we found that fencing had no impact on the responses of diversity indices along precipitation gradients but tended to increase them with increasing temperature (Appendix Fig. S2 and Table S1). On the other hand, environmental fluctuations might be more critical than fencing vs. grazing in shaping species diversity and ecosystem functioning as well as their relations (Milchunas and Lauenroth, 1993). As reported in previous studies, precipitation and its variability are the most limiting factors for community productivity on the Tibetan Plateau (Shen et al., 2015; Shi et al., 2014; Yang et al., 2010). Furthermore, plant species diversity and functional trait diversity can also be as crucial as precipitation in shaping the spatial pattern of productivity of alpine grasslands on the northern Tibetan Plateau (Wu et al., 2014b, 2016). Similar findings are also reported in global studies that plant species diversity is as strong as other key drivers of productivity in natural ecosystems, such as precipitation in grasslands (Duffy et al., 2017; Gaitan et al., 2014).

In addition, we found that BNPP was positively correlated with species richness (Fig. 5 e) but not related to the Shannon diversity index (Fig. 5 f). This might be due to that environmental (climatic) filtering (Batriu et al., 2015; Kraft et al., 2015; Le Bagousse-Pinguet et al., 2017) is very strong on species assembly and coexistence in this area (Fig. 1). For example, species richness declines with the increasing environmental severity of decreasing precipitation, increasing temperature, and decreasing soil nutrients and moisture from east to west across the northern Tibetan Plateau (Lu et al., 2015a; Wu et al., 2014b). Besides, plant competitions for the limited nutrients and moisture in soils drive alpine steppe and desert-steppe communities to be much sparser than alpine meadows (Zhu et al., 2015). The shallow-rooted sedge species,

i.e., *K. pygmaea* dominated in alpine meadows disappear in alpine steppes and desert-steppes, while the deep-rooted species, i.e., *Oxytropis glacialis* Benth. ex Bunge and *Ceratoides latens* Reveal & N.H. Holmgren, become more common in alpine steppes and desert-steppes. Therefore, the relationship of BNPP shifts from being linear with species richness to no relation to the Shannon diversity index. Moreover, this might be partly due to the specific responses of different life forms to changes in climate and land use (Batriu et al., 2015; Golluscio et al., 1998; Peters et al., 2014; Tarhouni et al., 2017).

4.3. Complexity and causality between climate, community productivity, and plant species diversity

A better understanding of grassland community responses to climate change and human disturbances requires more explicit explorations on the complexity and causal links between biotic and abiotic variables, particularly in low productivity environments (Deleglise et al., 2011; Erfanzadeh et al., 2015; Lezama et al., 2014; Travers et al., 2018). In our study, we found that plant species diversity indices are interacting with climatic variables to control local productivity partitioning of alpine grasslands on the northern Tibetan Plateau (Fig. 6), although the interaction between species richness and precipitation was not significant to impact BNPP (Fig. 6 and Table 3). This spatial complexity also agreed with the finding of Klanderud (2010) that a simple trajectory, linear or unimodal, is not necessary for natural grasslands to follow in their responses to climate change and grazing disturbance.

On the other hand, our findings of spatial complexity also indicated that the localized specific strategies of alpine grassland plants adapting to climate fluctuations and human disturbance should be addressed for better understanding the mechanisms behind the biodiversity-productivity (ecosystem functioning) relationship. For example, smaller plant species are generally thought to be more resistant to livestock feeding than taller grasses (Osem et al., 2004). However, prolonged heavy grazing by livestock in low productivity grasslands is likely to change plant community composition by altering the relative dominance of palatable vs. less palatable species through herbivores selective feeding (Lavorel et al., 1997). Moreover, in low-productivity

drylands the deep-rooted legumes that are tolerant of droughts and less palatable for livestock might boom due to long-term overgrazing while the shallow-rooted grasses that are sensitive to droughts but more palatable would likely to reduce (Ganjurjav et al., 2018; Lavorel et al., 1997; Muler et al., 2018).

In this study, we also tried to clarify the causality between climate, plant diversity, and productivity component by using structural equation models (Fig. 7). Precipitation was confirmed to have the most critical direct influences on species diversity indices and above-ground productivity (Fig. 7). This is consistent with previous studies that precipitation is the primary driver for species specification and community productivity on the northern Tibetan Plateau (Shen et al., 2015; Shi et al., 2014; Yang et al., 2010). However, BNPP was found to be not directly influenced by precipitation (Figs. 4e and 7b) but controlled by temperature and indirectly influenced via plant diversity indices at regional scales (Figs. 4f and 7b), being partly due to the profoundly negative correlation between temperature and precipitation across grasslands of the Tibetan Platea and Central Asia (Wang and Wesche, 2016).

Except for the direct links between productivity components and climatic variables, we also found that the indirect climatic effects via plant species diversity indices on productivity partitioning were considerable and should not be ignored. For example, the indirect influence of precipitation via species richness was found to positively influence aboveground productivity, which was a bit stronger than the negative indirect influence of precipitation via the Shannon diversity index (Fig. 7a). This indicates that species composition is likely more critical than species dominance in controlling aboveground productivity in Tibetan alpine grasslands. On the other hand, we found that climatic factors had weak indirect influences via plant species diversity indices on belowground productivity (Fig. 7b). Lamb (2008) has suggested that even though temperature mainly controlled species competition and root turnover rate in grasslands, belowground interactions is not essential as expected in structuring community diversity or productivity. The less variance of BNPP explained by structural equation models than that of ANPP (Fig. 7) might indicate more complex mechanisms on belowground ecosystem functions. Further studies should include more relevant biotic and abiotic variables for more holistic understandings of the biodiversity-productivity relationship with potential links between above- and below-ground organisms.

5. Conclusions

Productivity partitioning of alpine grasslands does not follow a simple smoothing, linear model or unimodal trajectory, in response to environmental changes in climate, plant diversity, and livestock management at a regional scale. Plant diversity indices can interact with climatic conditions to control local productivity partitioning in a nonlinear and networking way. Land use change, shifting from grazing to fencing, cannot significantly alter the manner of productivity components responding to regional changes in climate variables and plant species diversity. The productivity partitioning between above- and below-ground for alpine grasslands on the northern Tibetan Plateau might be the outcome of highly-localized species and well-evolved plant traits to adapt to severe climate and livestock grazing. Finally, we recommend using a joint approach of generalized additive models and structural equation models to better understand the complexity and causality of ecosystem responses to climate change and human disturbance in other grasslands all over the world.

Author contributions

JW conceived and designed the experiment. JW, ML, WM, and XW collected data in the field. JW, ML, and WM analyzed the data. JW prepared the figures and led the writing. SF, XW, BT, and XZ revised the text and interpreted the results. All authors contributed to this work and

approved the final manuscript. The authors declare that they have no competing interests.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2018.10.097.

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